

# Notes on Atlantic and other Asteroidea. 3. The families Ganeriidae and Asterinidae, with description of a new asterinid genus

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## Introduction

Examination of new and old material of these two closely related starfish families has prompted some additional observations on their limits and relationships, with consequent modifications to the diagnoses. A notable addition in the Ganeriidae is the abyssal genus *Vemaster* Bernasconi, 1965, formerly assigned to the Goniasteridae, but now shown by dissection of new specimens to be more closely related to *Ganeria*, a move supported by Downey and Blake (pers. comms). Several of the nominal genera proposed by Verrill (1913) for the Asterinidae are reevaluated, resulting in the synonymy of *Patiria* with *Asterina* and, conversely, in the revival of *Callopatiria*. Some recently collected asterinids from the Atlantic coast of Panama proved to represent a new genus remarkable for having many of the abactinal plates paxilliform.

A difficulty arose in formally citing the type species of *Asterina* itself, for which a possible solution to the nomenclatural problem is given in an appendix.

## Systematic account

### Families *GANERIIDAE* Sladen and *ASTERINIDAE* Gray

Blake (1981) has reviewed the history of these two families which he transferred to the order Valvatida from the Spinulosida. Briefly, Gray (1847) originally included *Ganeria* itself in his Asterinidae, being followed in this by Perrier (1875) and Viguier (1878). However, Sladen (1889) distinguished the subfamily Ganeriinae within the Asterinidae, on the basis of enlarged marginal plates, for *Ganeria* and *Cycethra* Bell, 1881 and this was raised to family rank by Perrier (1894). Later authors, notably Fisher (1911a) and Blake (1981), have emphasized the close affinity between the Ganeriidae and the Asterinidae. Fisher followed Sladen in distinguishing them on the basis of large size of the marginal plates in ganeriids but this does not take account of those individuals of *Cycethra* and all the species of the later-added *Perknaster* in which the marginals are reduced and the series may be barely, if at all, distinguishable over part of their extent. Bernasconi (1964) and Blake (1981) have separated them on the form of the abactinal plates, with well defined columns of various height in the Ganeriidae but with ridge-like elevations or gently rounded convexities in the Asterinidae (though Blake termed both plate forms 'metapaxilliform' since the basal part of each plate is variously enlarged and the elevation often excentric) but this again does not take into account the amazing variations of *Cycethra*, some individuals of which have simply convex or crescentic elevations indistinguishable from those of certain Asterinidae instead of the usual well-defined but low columns ranging from circular through oval to crescentic in section. Blake also utilized the arrangement of these plates, said to be in ill-defined rows in Ganeriidae but well-defined ones in Asterinidae; however, some asterinids, especially those of large size comparable to that of many specimens of *Ganeria* and *Cycethra*, have an essentially alternating abactinal skeleton, though alternate plates may have a secondarily longitudinal alignment, for instance in *Patiria granifera* (Fig. 6, below) and *Nepanthia crassa*.

In an attempt to assess the relationships of the various plate systems of Atlantic asteroids,

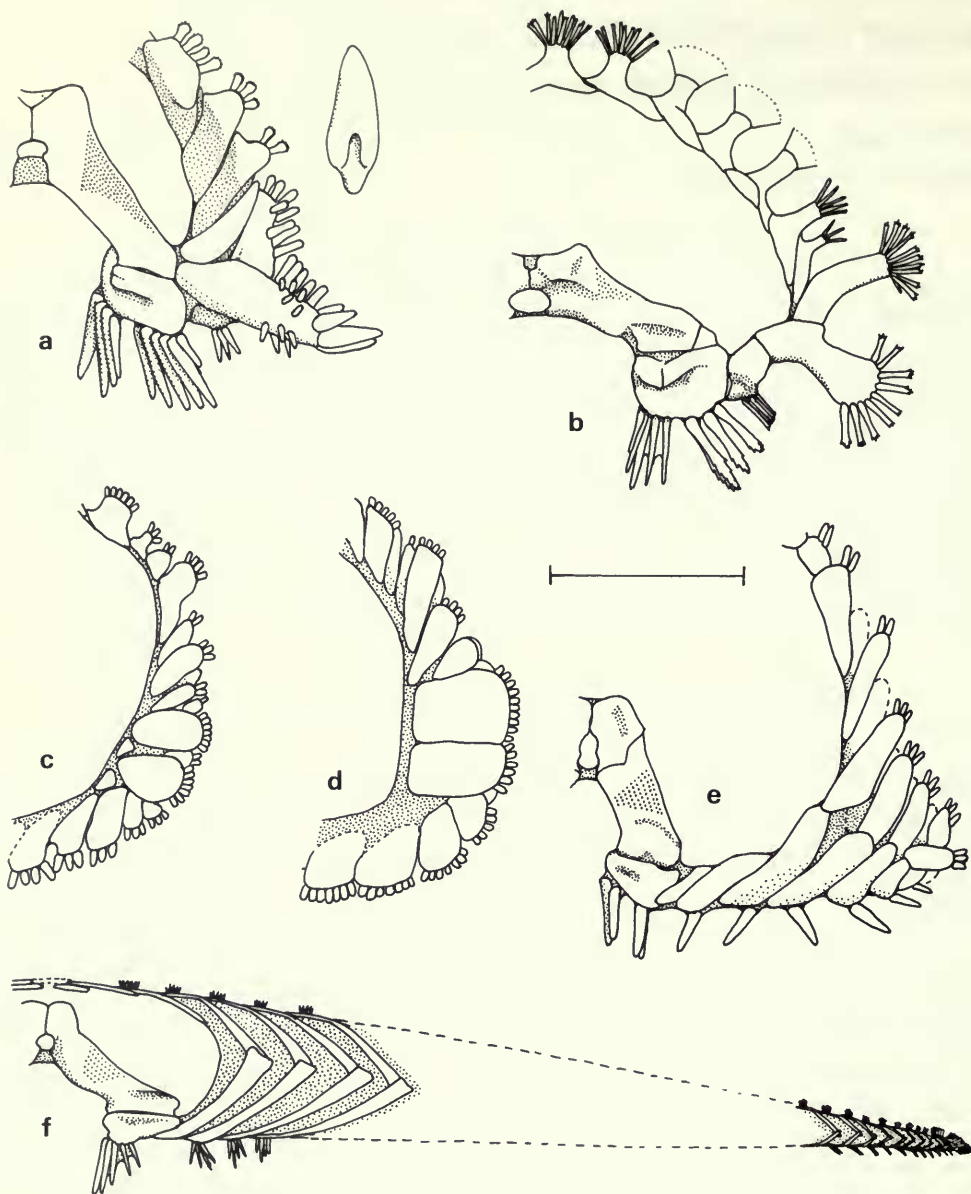


Fig. 1 Partial cross sections near base of ray viewed from proximal side of : (a) *Leilaster radians* (Perrier), *Gerda* st. 1270. Yucatan Channel, W of Cuba, 318 m, R 11.5–14.5 mm (with isolated inferomarginal plate viewed from above); (b) *Lophaster furcifer* (Düben & Koren), BM reg. no. 91.5.20.1, Trondheim fjord, R 30 mm; (c) *Cycethra verrucosa* (Philippi), 1971.9.1.4, N Argentina, R 40 mm; (d) *C. verrucosa*, formerly named *Patiria obesa*, 1948.3.16.356, mid-Argentina, R 33 mm; (e) *Asterina gibbosa* (Pennant), 98.5.3.171, Falmouth, Cornwall, R 15.5 mm; (f) *Anseropoda placenta* (Pennant), 88.10.8.1, W of Scotland, R 31–40 mm (oblique section following the lines of abactinal and actinal plates). Plates not in the plane of the section shown by discontinuous lines except in (f). The scale measures 2 mm for (a), 2.5 mm for (e) and (f), 3 mm for (b)–(d).

I have made cross-sections of the rays of some taxa. Where the Ganeriidae and Asterinidae are concerned, these do show considerable resemblances between some species of both families but I find there is always a more or less well-defined ventro-lateral angle at the level of the inferomarginal plates in the Asterinidae, whereas in ganeriids the contour of the ray in this area is curved, the actinal surface being slightly convex and merging into the side of the ray. Inevitably, in asterinids such as *Nepanthia*, where the well-defined arms are nearly cylindrical, the angle is least, but it is still distinct. Coupled with the superficial shape, the marginals of the Ganeriidae, when enlarged, are block-like, these of the two series similar in form and not wedged in by internal extensions of the lateralmost abactinal and actinal plates. In the Asterinidae the marginals of the two series are consistently small and often only recognizable by their regularity along the angle (the superomarginals sometimes barely distinct), the flattened inferomarginals appearing pearshaped or pegshaped in the sectional view and wedged in by the inner ends of the adjacent plates or some supernumerary internal plates which form a series of buttresses or a more continuous structure reinforcing the ventro-lateral angle (see Fig. 1e, 5b, c). In the extremely flattened asterinid *Anseropoda* the ventro-lateral angle is very narrow and the reinforcement for the upper side spans almost the entire body cavity of the ray, except for a narrow midradial area, taking the form of angled struts in obliquely transverse series, each made up by a slender flattened process from an abactinal plate overlapping the upper end of a similar process from the corresponding actinal plate (Fig. 1f).

One consequence of this study is realization that *Leilaster* A. H. Clark, 1938 is not a ganeriid. When established by Clark for type species *Korethraster radians* Perrier, 1881, from the Caribbean, Fisher evidently supported a proposal to include it in the Ganeriidae. He reiterated this in 1940 (pp. 152–153) when discussing the antarctic *Mirastrella*, which he referred to the Asterinidae though commenting that the 'produced inferomarginals' also suggested affinity with the Ganeriidae. Presumably he could then only have had *Leilaster* in mind, not the true ganeriids. A cross-section of a ray of the small *Leilaster radians* (Fig. 1a), where R is up to only c. 15 mm, shows a flat underside formed mainly by the relatively large cigarshaped inferomarginal plates which abut directly on to the outer ends of the ambulacral plates (the single actinal plate in a proximal section being superimposed). As viewed from above, the inferomarginals are slippershaped, tapering outwardly, and have a notch on the inner (adradial) half forming a socket into which fits the lower end of the vertically aligned corresponding superomarginal plate. The coarse abactinal plates imbricate adradially (the more lateral ones) or proximally (the midradial ones) and each is raised into a ridge or rounded column and crowned with coarse capitate spinelets. The formation of a lateral flange to the body made by the inferomarginal plates and the imbricating abactinals are characters shared with most asterinids but in *Leilaster* the inferomarginals are relatively much larger and nothing like their articulation with the superomarginals is shown in the asterinids studied, nor do they directly contact the ambulacral plates in asterinids without multiple series of intervening actinal plates—even at this relatively small size. Further, in *Leilaster* the proximal articulating face of the adambulacrals (which provides characters given considerable weight by Blake) is rectangular and has a complex near-horizontal groove unlike any of the squarish, slightly hollowed adambulacrals of the asterinids and other Valvatida studied.

These internal structures have yet to be studied in *Mirastrella biradialis* Fisher when more material is available. Consultation with Miss M. E. Downey of the Smithsonian Institution, co-author of the review of Atlantic Asteroidea for which the present note is a preliminary, yielded her opinion that *Leilaster* and *Mirastrella* are closely related. They share two unusual characters not shown by any ganeriids or asterinids. For one thing, there is a distinct groove (or fasciole) in each interradius running vertically from the margin up to the flat top of the disc between the two first superomarginals and the interradian abactinal plates above. Secondly, there are two longitudinal (but bowed) series of enlarged abactinal plates (the 'first adradial' series of Fisher) on each ray framing the three (*Leilaster*) or two (*Mirastrella*) longitudinal series of midradial plates like the two prongs of a wishbone.



The complex articulating face of the adambulacrals in *Leilaster* shows some resemblance to that of the spinulosan *Lophaster furcifer* (Düben & Koren) of the family Solasteridae (Fig. 1b). *Lophaster* also has reduced actinal areas, though the section made shows one actinal interposed between the inferomarginal and the ambulacral/adambulacral articulation, at least in the proximal part of a ray at R c.30 mm. The superomarginal in *Lophaster* has a tall paxillar column and a triradiate base, two lobes of which articulate with the upper side of the expanded adradial part of the inferomarginal straddling a median hollow which does not form a socket. The marginals as well as the abactinal plates in *Lophaster* and other solasterids are highly paxilliform with slender rounded columns, rather than being metapaxilliform as in *Leilaster*. Even so, I think Verrill (1915) had some justification for treating a specimen with R 35 mm, three times that of the type of *L. radians*, as conspecific; his specimen was renamed *Lophaster verrilli* by A. H. Clark in 1938. Whether or not the small specimens which have been referred to *Leilaster radians* and *Mirastrella biradialis* should be referred to the Spinulosida remains to be determined from a review of that order.

Another genus of uncertain affinities is the diminutive abyssal *Vemaster* Bernasconi, 1965, from the Argentine Basin (maximum R only 15 mm). Because of some resemblance in the tabulate abactinal plates to *Cladaster* and *Nectria* Bernasconi referred *Vemaster* to the Goniasteridae. However, examination of some additional material of *Vemaster* shows that the superomarginal plates are undeveloped and the inferomarginals displaced to a ventrolateral position and not at all blocklike (both marginal series being essentially well-developed and blocklike in Goniasteridae), there is no regularity in the arrangement of the abactinal plates and the actinal plates are very reduced and irregular, being possibly secondary calcifications. Also, internally *Vemaster* has an archlike calcified interbrachial column arising from near the oral plates in each interradius, curving laterally at its upper end to meet the lateral wall of the disc, this compares with a solid calcified interbrachial buttress fused to the side of the disc in *Nectria*, which genus also has superambulacral plates developed (according to Fisher, 1911a), not observed in *Vemaster*, besides having regularly arranged abactinals. However, just such an inclined columnar interbrachial support is found in Ganeriidae such as *Cycethra* and *Perknaster* (indeed in the specimen of *P. sladeni* studied, this structure is arched over as in *Vemaster*), which genera also show a marked tendency for reduction of the marginals and loss of their blocklike form, especially *Perknaster*, where the abactinal plates are irregular and the actinal areas somewhat reduced.

Apart from the much finer abactinal skeleton of *Perknaster*, the main difference between it, together with the other southern genera of Ganeriidae, and *Vemaster* is the absence of a ventrolateral angle—emphasized above as a characteristic feature of the family in comparison with the Asterinidae—whereas the inferomarginals of *Vemaster* form a distinct projection in this area, the arms being D-shaped in cross-section with the ventral side quite flat. The asterinid *Nepanthia* does have an almost D-shaped arm section but here actinal plates are developed in regular series on the arms and superomarginals combine with the inferomarginals to make the ventrolateral angle.

Both Downey and Blake (pers. comms) support reference of *Vemaster* to the Ganeriidae. However, in view of the marked difference in arm section, I think that its isolation in a separate subfamily from the closely related *Ganeria*, *Cycethra* and *Perknaster* may prove to be desirable. This problem must await comparison of all these with other genera from parts of the world outside the Atlantic which have been referred to the Ganeriidae but which seem to me less closely interrelated than are the three Southern Ocean genera. These other genera are: *Aleutiaster* A. H. Clark, 1939, from the Aleutian Is, North Pacific, *Hyalinothrix* Fisher, 1911b, from the Hawaiian Is, *Knightaster* H. E. S. Clark, 1972, from New Zealand and *Tarachaster* Fisher, 1913, from the Philippines with a second species from New Zealand of McKnight, 1973, the rest being monotypic.

Another taxon which the study of arm sections shows to have been misplaced is *Patiria* (originally *Parasterina*) *obesa* (H. L. Clark, 1910), recorded from both sides of southern South America. In 1962 I renamed as *P. obesa* four *Discovery* specimens from southern Argentina (which Fisher (1940) had identified as *Cycethra verrucosa* forma *nitida*) since they



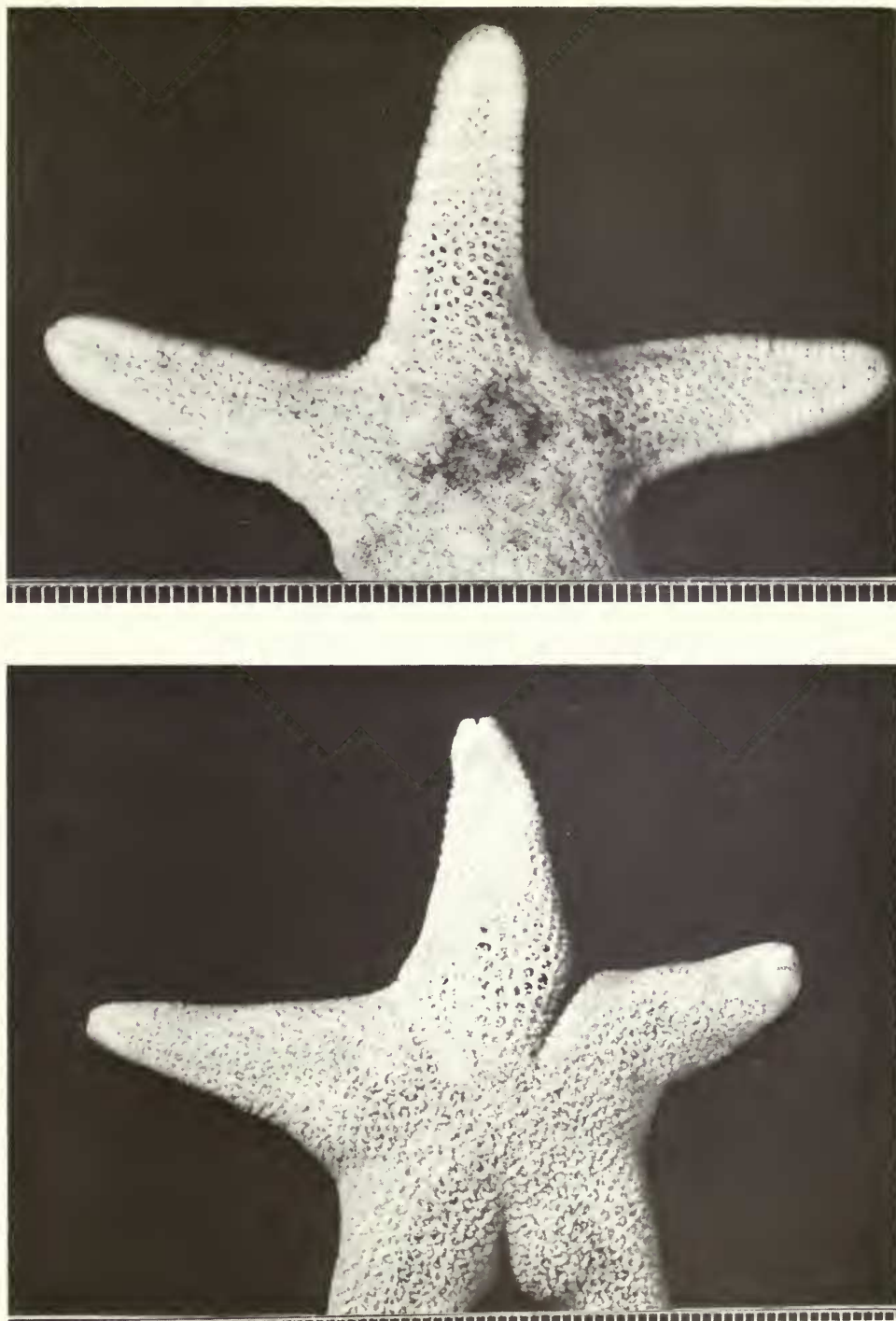


Fig. 2 *Cycethra verrucosa* (Philippi), BM reg. no. 1948.3.16.356, Argentina, R 33 mm (formerly named *Patiria obesa*),  $\times 2$  (above) and 1948.3.16.344, W Falkland I, R 39 mm, with more abrupt elevations on the abactinal plates but reduced marginals,  $\times 1\frac{1}{2}$  (below).

closely resemble the photographs of H. L. Clark and of Madsen (1956) of *P. obesa* from Chile and have notably asterinid-like abactinal plates with only low crescentic convexities, though some of them have the distal superomarginals enlarged in an 'un-asterinid-like' way (fig. 2 top). Madsen also recorded an Argentinian specimen as *obesa* and noted that the development of the marginals varies from barely distinct (as in the holotype) to fairly conspicuous, as in the *Discovery* specimen sectioned (Fig. 1d) and even more the one photographed. These marginals are block-like and those of the two series similar in shape, forming a curved surface with no sign of an angle at the inferomarginal. Bernasconi too (1973) found the marginal area of *obesa* to be thick and rounded. Such a form matches that of some specimens of *Cycethra verrucosa*, in which species the marginals show a similar wide range of development, whereas in asterinids the marginals variously developed have been found to have the abactinal plates variously developed with elevations ranging from ill-defined columns to crescentic rounded convexities. I must therefore concede the correctness of Fisher's identification of the *Discovery* specimens, from which it follows that *Patiria obesa* is yet another synonym of *Cycethra verrucosa* (Philippi, 1857), a taxon so variable that I think it futile to try and treat *Cycethra* as other than a monotypic genus.

Madsen and Bernasconi both compared *P. obesa* with *P. bellula* Sladen of South Africa, the type species of *Callopatiria* Verrill, 1913, synonymized with *Patiria* by Fisher (1940); Madsen suggested 'perhaps this genus [*Callopatiria*] ought to be retained and also include the species *obesa*', an idea supported by Tortonese (pers. comm.). I too agree that *Callopatiria* deserves recognition, as discussed below, and think it comes closest of all the asterinids to *obesa*, though I am convinced that the true place of *obesa* is among the Ganeriidae.

In his drastic summary revision of the Asterininae (1913), Verrill recognized no less than 12 nominal genera in addition to *Stegnaster* and *Tremaster*, since isolated in a separate subfamily, four of them unconnected with the Atlantic fauna, leaving the following for consideration:

*Asterina* Nardo, 1834. Type species (see appendix, p. 378): '*Asterias minuta* = *A. gibbosa* (Pennant, 1777)' by subsequent designation by Fisher, 1906.

*Asterinides* Verrill, 1913. Type species: *Asteriscus folium* Lütken, 1860.

*Patiria* Gray, 1840. Type species: *P. coccinea* Gray, 1840, a synonym of *Asterias miniata* Brandt, 1835.

*Patiriella* Verrill, 1913. Type species: *Asterina regularis* Verrill, 1867.

*Asterinopsis* Verrill, 1913. Type species: *Asterias penicillatus* Lamarck, 1816.

*Enoplopatiria* Verrill, 1913. Type species: *Asteriscus marginatus* Hupé, 1857, a nom. nud. conspecific with *A. stellifer* Möbius, 1859.

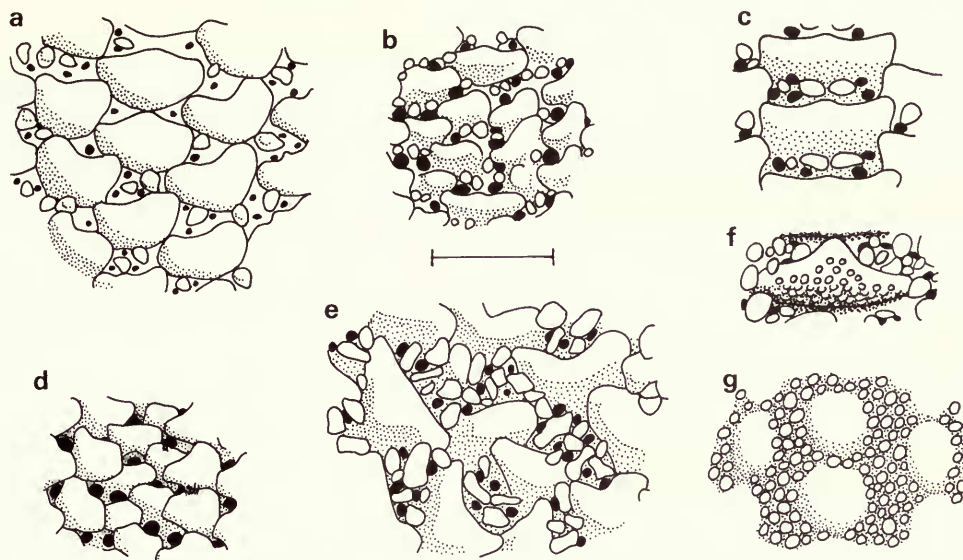
*Callopatiria* Verrill, 1913. Type species: *Patiria bellula* Sladen, 1889, a synonym of *P. granifera* Gray, 1847.

*Allopatiria* Verrill, 1913. Type species: *P. ocellifera* Gray, 1847.

Of these, *Asterinides* has been synonymized with *Asterina* by Fisher (1919), in his Philippine book, on the grounds that the absence of pedicellariae (the only distinction given by Verrill) is not a character of generic weight. However, Brito (1968) apparently overlooked this and Tommasi (1970) disregarded it, both of them retaining *Asterinides* for *folium* without further justification. Although occurrence of pedicellariae is unreliable even as a specific character, the name *Asterinides* might be utilized, at least at the subgeneric level, for a group of species with the body relatively low and near pentagonal (though this alone is not of supraspecific weight) correlated with very fine, easily detached abactinal spinelets. Besides *A. folium* it could also include the Indo-Pacific *sarasini* group of species discussed in Clark & Rowe (1971: 67-68).

Verrill (1913; 1914a & b) differentiated his nominal genera only in two versions of a dichotomous key, the 1913 one confused by the omission of one option: DD. 'Interactinal plates without a fan of spines', which I think should have come on p. 480 after *Enoplopatiria* and been immediately followed by b and bb (for *Patiriella* and *Asterinopsis*) though Verrill

(1914a) proposed its insertion on p. 479 after EE and before x for *Patiria* which *does* have fans of spines on the actinal plates. It appears that *Enoplopatiria*, resulting from xx, must have been an afterthought, since the sequence in the key is otherwise alphabetical from A to G. The 1914b version shows Verrill's true intention and this was clarified by Fisher (1919), who adopted *Patiriella* and produced a simplified key to the Pacific genera of Asterininae, differentiating *Patiriella* and *Patiria* from *Asterina* by the abactinal structure, simpler in *Asterina* with the plates of the papular areas of only one kind and rounded, elliptical, cordate or shieldshaped (in Verrill's words), as opposed to plates of two or more diverse kinds, the larger arched or crescentic and notched for the papulae and the smaller ones ovate or pear-shaped and inserted endwise (vertical to the surface) between the larger.



**Fig. 3** Denuded abactinal plates from proximal part of midradial area of: (a) *Asterina gibbosa* (Pennant), BM reg. no. 1960.8.4.4, Syra, Aegean Sea, R 27 mm; (b) *Asterina* (formerly *Patiria*) *miniata* (Brandt), 1954.9.8.43, San Pedro, S California, R 16 mm; (c) *Patiriella regularis* (Verrill), 1970.10.8.111, Nelson, New Zealand, R 21 mm; (d) *Asterina folium* (Lütken), USNM no. 38811, Sand Key Reef, S Florida, R 8 mm (a few surviving spinelets shown at the proximal ends of two plates); (e) *Callopatiria* (formerly *Patiria*) *granifera* (Gray), 1903.8.1.47, Mossel Bay, S Africa, R 40 mm; (f) *Asterina* (formerly *Patiria*) *stellifera* (Möbius), 1936.10.14.3, Accra, Ghana, R 41 mm; (g) *Allopattiria ocellifera* (Gray), 1969.12.16.13, Cape Lever, Mauritania, R 38 mm. The scale measures 4 mm for (g) and 2 mm for the rest; (a) and (f) are from wet specimens, the pores appearing relatively small.

However, examination of a relatively large specimen of *Asterina gibbosa* (R 27 mm) (Figs 3a, 4 top) shows closer agreement of the abactinal skeleton with the second option than the first, there being two or even three small secondary plates in some of the papular areas and the primaries in the papular areas *are* mostly crescentic. The type species of both *Patiria* and *Patiriella* reach a considerably larger size, R > 60 mm, and develop many more secondary plates though at R < 30 mm these are relatively few in number (Fig. 3b, c). The form and arrangement of the other plates, including the internal ones buttressing the lateral angles of the arms (see Fig. 1e), and the armament of *A. gibbosa* and the other two type species, do not seem to me significantly different, while the difference in maximum size alone seems inadequate for the distinction of genera. Verrill's keys tried to distinguish *Patiriella* from *Asterina* also by the reduced actinal armament of usually only a single spine, rarely more



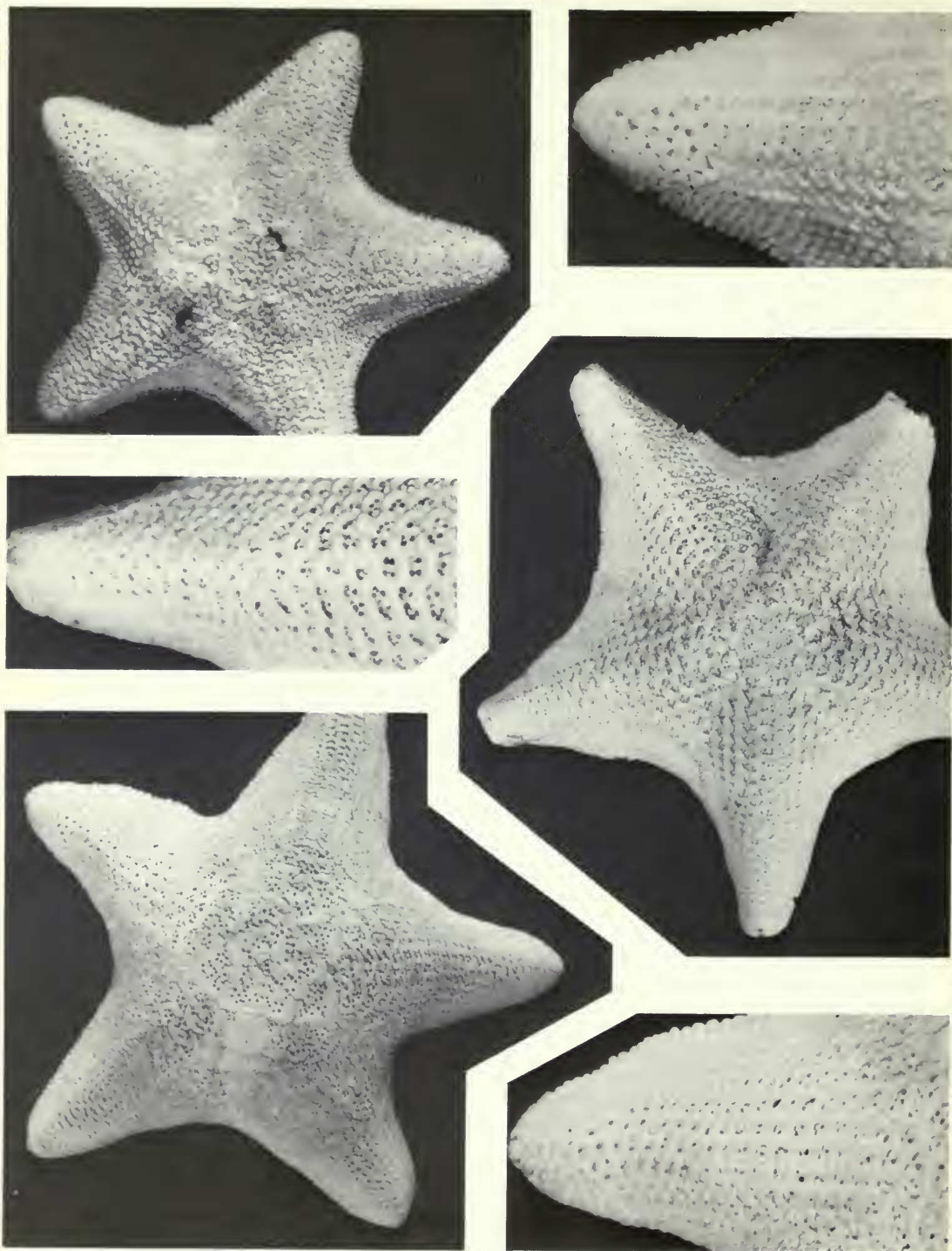


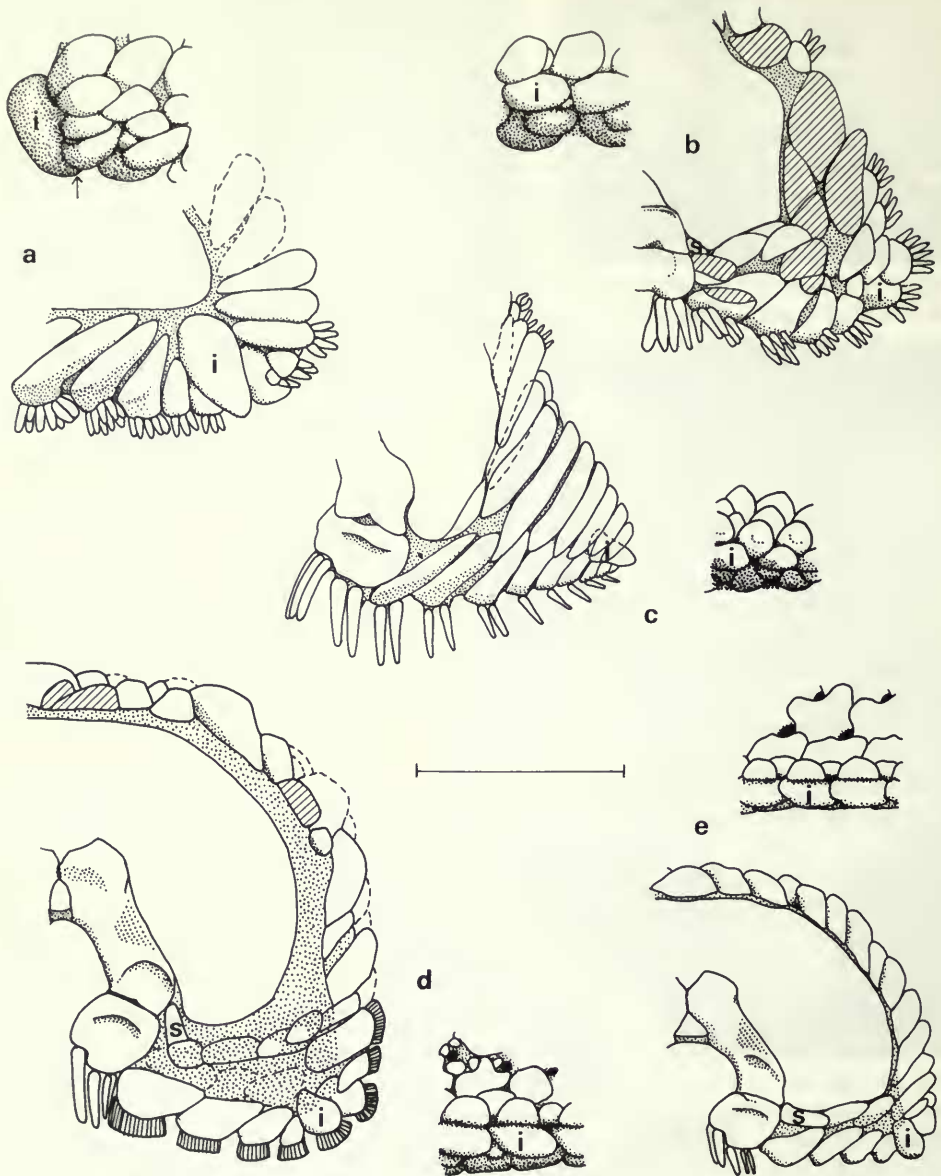
Fig. 4 Dorsal views,  $\times 1\frac{1}{2}$ , and enlargements of denuded rays,  $\times 3$ , of: *Asterina gibbosa* (Pennant), BM reg. no. 1960.8.4.4, Syra, Aegean Sea, R 27 mm (above); *Asterina* (formerly *Patiria*) *miniata* (Brandt), 1954.9.8.43, San Pedro, California, R c.32 mm (middle); *Patiriella regularis* (Verrill), 1970.10.8.112, Golden Bay, New Zealand, R 30 mm (below).

than two on a plate. Dartnall (1971) in diagnosing *Patiriella* also noted that the abactinal armament is short, granular and bluntly capitate, the carinal (midradial) plates are doubly notched to accommodate two longitudinal rows of papulae and pedicellariae are lacking. The other characters he mentioned are common to *Asterina gibbosa* and indeed some of the midradial plates in that species also subtend two pores though the three proximal lobes are less marked than in *Patiriella regularis*. Small specimens of *A. gibbosa* and many *A. burtoni* Gray, for instance, also have no more than two actinal spines. However, the particularly coarse and abbreviated abactinal armament in the australasian species *P. regularis* and *P. gunni* (Gray), as well as the pan-oceanic *P. exigua* (Lamarck), and perhaps the frequent development in these of a regular pair of secondary plates proximal to some of the trilobed midradial primaries (not observed in *A. gibbosa*), may serve to justify retention of *Patiriella* with generic (or perhaps subgeneric) rank. Dartnall (pers. comm.) shares my doubts about the generic distinction of *Patiriella*. Since Australia is rich in species of both *Patiriella* and *Asterina*, the resolving of this problem seems best left to one of the several interested Australian specialists, the name *Patiriella* being retained here for *P. exigua* which extends to St Helena.

*Patiria miniata* from the NE Pacific was only shown to be the type species of *Patiria* in 1933 when Mortensen synonymized with it *P. coccinea* Gray, mistakenly recorded from South Africa. Fisher (1911a), in his N Pacific asteroid monograph, had included *miniata* in *Asterina* and this combination has been perpetuated in the Pacific literature for both *miniata* and the closely related Japanese *pectinifera* (Müller & Troschel). These two differ from *Asterina gibbosa* (apart from the greater maximum size) in lacking pedicellariae but this is not true of *P. stellifera* (Möbius), the type species of **Enoplopatiria**, from E South America and W Africa, which is otherwise very similar to *P. miniata* in shape, plate structure and armament. *Enoplopatiria* was synonymized with *Patiria* by Fisher (1919), discounting the taxonomic weight of the occurrence of pedicellariae, as with *Asterinides*, but *Enoplopatiria* was similarly retained by some South American authors, in this case Bernasconi (1955), as well as Brito (1968) and Tommasi (1970). However, Madsen (1950) had used *Asterina* for *stellifera* and this was followed by me in 1955. Subsequently I expressed doubts (quoted by Tommasi) about this position for *stellifera* because of the many secondary abactinal plates and, in Clark & Courtman-Stock (1976), like Tortonese (1956) and Bernasconi (1966), used *Patiria stellifera*. I am now forced to the reverse, rejecting greater maximum size and its commensurate elaboration of the abactinal skeleton as justifying a generic distinction; both *Enoplopatiria* and *Patiria* itself are therefore to be synonymized with *Asterina*.

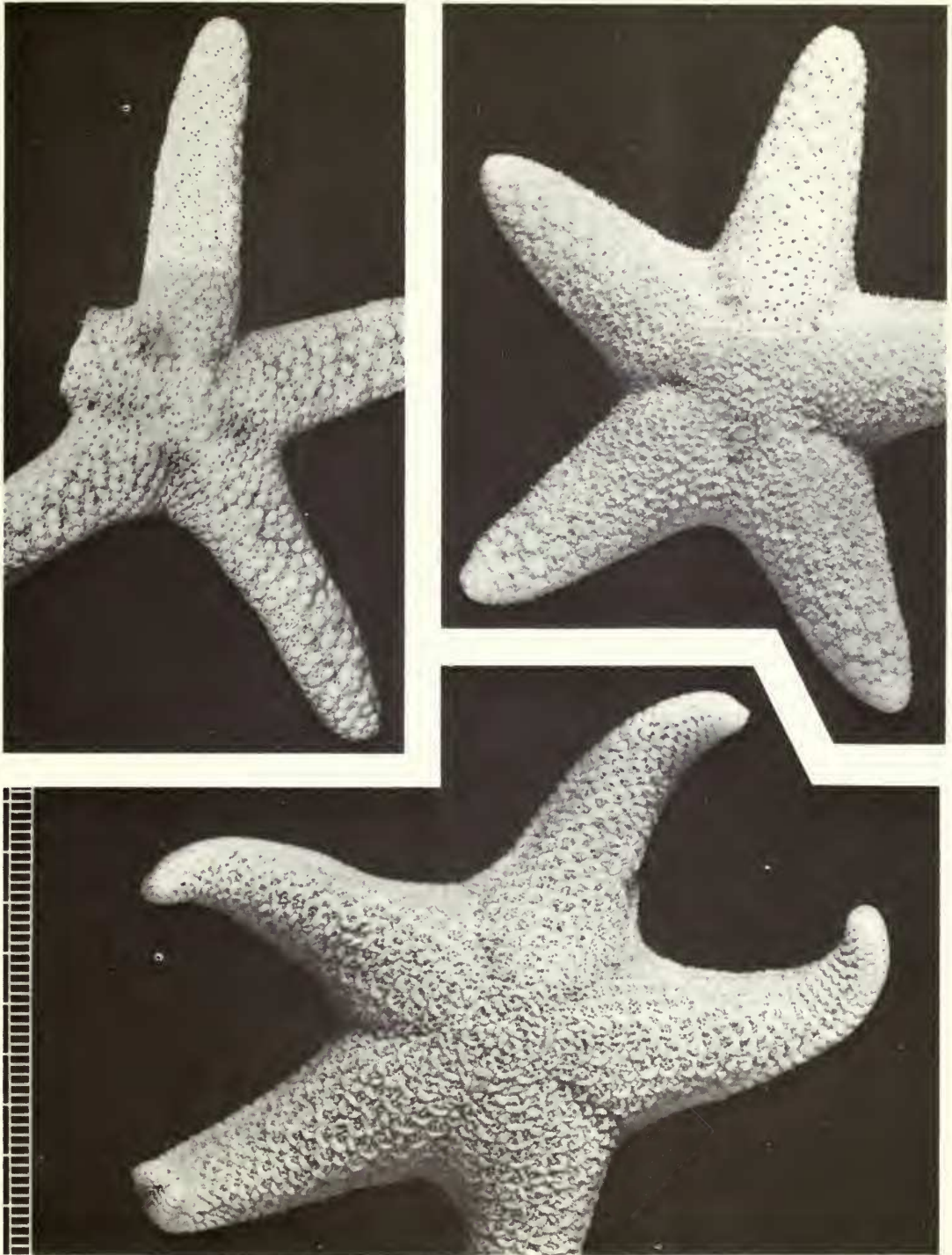
Of the remaining species currently included in *Patiria*, *P. obesa* (H. L. Clark, 1910) is referred above to the synonymy of *Cycethra verrucosa*, *P. granulosa* (Perrier, 1875), supposedly from the Hawaiian Is, was based on specimens which appear to be conspecific with *P. miniata* (indeed, one sample is so referred in the catalogue of the Paris Museum collections) and *P. chilensis* (Lütken, 1859) is also close to *miniata* and so falls within *Asterina*. This leaves only *P. granifera* Gray, 1847 and *P. formosa* (Mortensen, 1933), both from South Africa, *P. obtusa* Gray, 1847, supposedly from Pacific Panama and *P. pulla* and *P. rosea* both of Koehler & Vaney, 1906, from Mauritania, these last two dealt with below under *Allopatiria*.

*Patiria granifera* is type species (by synonymy with *C. bellula*) of **Callopatiria**, which was formally synonymized with *Patiria* by Fisher in 1941, since Mortensen (1933) cited *C. bellula* in the references to [*Parasterina*] *bellula* and Fisher himself (1940) returned *bellula* to *Patiria*. In 1956 I synonymized *bellula* with *granifera*. Comparison of arm sections of this species with *Patiria* (or *Asterina*) *miniata* now shows a significant difference in the alignment of the superomarginal plates, those of *P. granifera* and the closely related *P. formosa* having both superomarginal and inferomarginal plates projecting to a similar degree together forming the ventrolateral angle (Fig. 5b)—whereas in *Asterina* sensu lato, *Patiriella* and *Allopatiria*, the angle is sharper and formed only by the inferomarginal series projecting beyond the inset superomarginals which may be hardly distinguished from the adjacent abactinal plates and can alternate in position with the inferomarginals along the arm. Of



**Fig. 5** Partial cross sections near base of ray viewed from proximal side, with lateral views of marginal area immediately distal to section, of: (a) *'Patiria' obtusa* Gray, holotype, BM reg. no. 1938.6.23.24, Panama, R up to 54 mm (the arrow shows the plane of the section where the internal part of the inferomarginal is exposed); (b) *Callopatiria* (formerly *Patiria*) *granifera* (Gray), 81.6.22.14, Cape Town, R 29 mm; (c) *Asterina* (formerly *Patiria*) *stellifera* (Möbius), USNM, Angola, R c.35 mm; (d) *Nepanthia crassa* (Gray), 61.7.8.32, Fremantle, Western Australia, R 40 mm; (e) *N. brevis* (Perrier), 81.10.26.172, Albany I, N Australia, R 28 mm. The parallel rows of dots on the ambulacral plates show the hyaline areas over which the tube foot slides; hatching shows cut surfaces of plates and discontinuous lines indicate plates not in the plane of the section; in (d) the outlines of the plates buried in the body wall are hypothetical. The scale measures 3 mm.





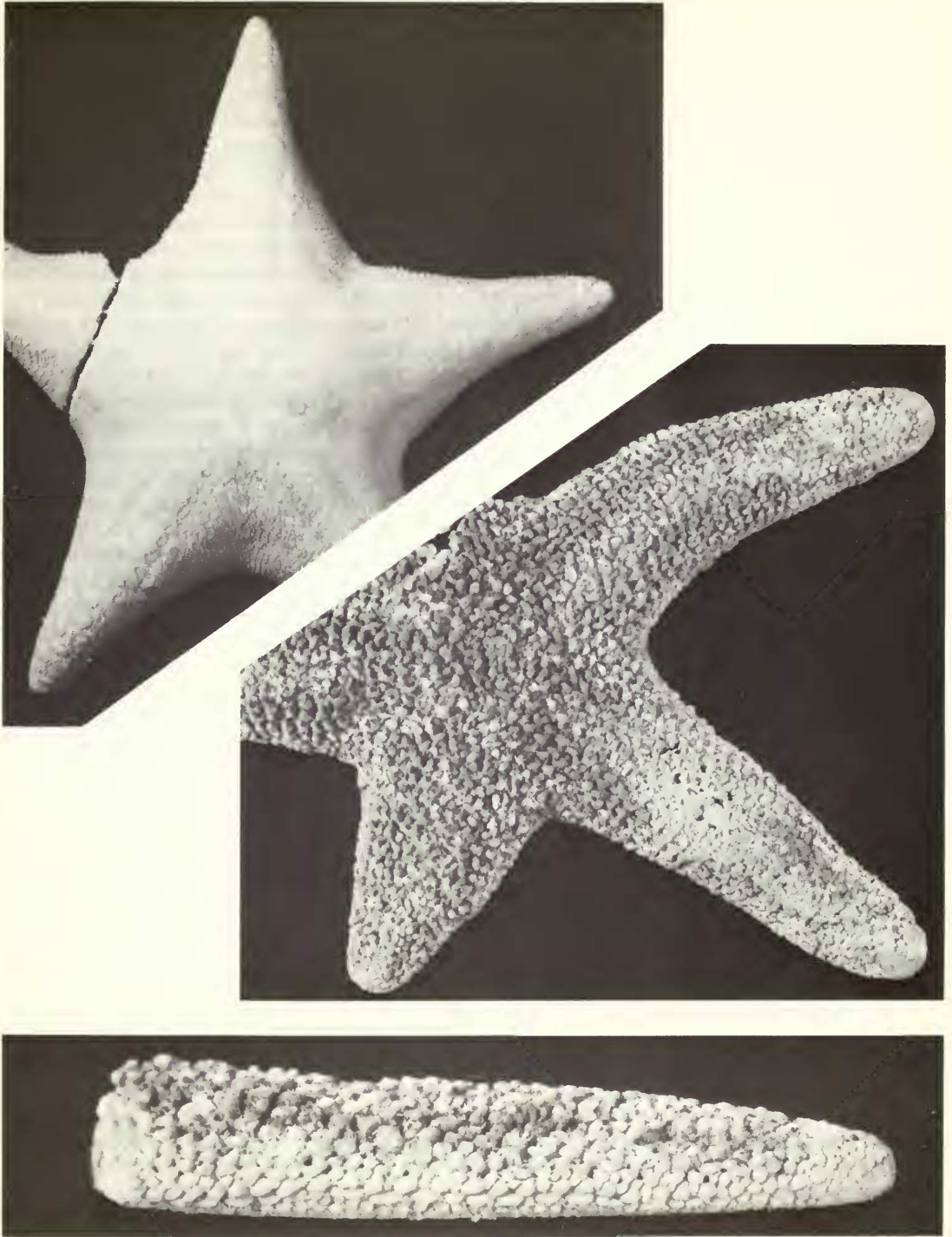
**Fig. 6** *Nepanthia crassa* (Gray), BM reg. no. 61.7.8.32, Fremantle, Western Australia, R c. 38 mm (above left); *Callopatiria* (formerly *Patiria*) *formosa* (Mortensen), 1975.10.29.62, False Bay, South Africa, R 36 mm (above right); *Callopatiria* (formerly *Patiria*) *granifera* (Gray), 1948.3.16.798, Saldanha Beach, South Africa, R 45 mm (below). All  $\times 1\frac{1}{2}$ .

the Asterininae studied, only in the Indo-Pacific *Nepanthia* does the marginal structure approximate to that in *P. granifera* and *formosa*, the sides of the ray being approximately vertical and the angle rounded, especially in species such as *N. belcheri* (Perrier) with thicker body walls and more numerous secondary abactinal plates.

Several other differences mark off *P. granifera* and *formosa*, together with *Nepanthia*, from the rest of the Asterininae under discussion. Firstly, the primary abactinal plates along the midradial line in the former are all crescentic or rounded and have an alternating or irregular arrangement whereas in larger specimens of *Asterina gibbosa* and other Asterininae some of these plates are proximally trilobed and tend to form at least a partial single longitudinal row, though this may be double for some of its length (Figs 3a–c, f). Secondly, some of the secondary abactinal plates are elongated in the superficial plane instead of vertical to it in the South African species and the *Nepanthia* species where such plates are numerous. Lastly, and perhaps most importantly, the transverse sections show that there are internal ventral plates bracing the ambulacrals by linking them with the actinals and other additional plates integrated with the ventrolateral angle, the adradialmost of which are equivalent to superambulacrals. In *Nepanthia brevis* (at least in the holotype) the superambulacrals are fairly regular in size and position and, in the proximal part of the arm at least, link through two other internal plates overlying the actinals to the lateral bodywall (Fig. 5e). However, in the specimen of *Patiria granifera* sectioned, these plates are less well developed and not regularly aligned, being also partly immersed in the fleshy internal part of the ventral bodywall (Fig. 5b). In *Nepanthia crassa* (formerly *Parasterina* but provisionally referred to *Nepanthia* by Fisher (1941) and confirmed there by Rowe & Marsh, 1982) there is massive ventral thickening of the body wall reinforced with irregular plates, some acting as superambulacrals, more or less deeply embedded in the soft tissue (Fig. 5d). *N. crassa* also carries to an extreme for *Nepanthia* the number of secondary (and even tertiary) abactinal plates. At the same time, its primary abactinals develop a more rounded than crescentic form compared with other *Nepanthia* species such as *N. belcheri*, such a modification having a parallel in *P. formosa* as opposed to the *P. granifera* (and indeed in *Allopatiria ocellifera* as opposed to the geographically adjacent *Asterina stellifera*). Marsh (pers. comm.) confirms the presence of obscured superambulacrals in *N. crassa* and has also found them in *N. maculata* and *belcheri*. This structure contrasts with the other Asterininae where the reinforcing plates for the ventrolateral angle do not extend adradially to help support the ambulacrals arch (see Figs 1e, 5c). Blake (pers. comm.) suggests that the development of superambulacrals in this instance is correlated with the relatively narrow and more nearly cylindrical arms, compared with most asterinids. The two South African species approximate to *Nepanthia* in body form, though the arms broaden slightly at the base to make blunt-angled or rounded interradiar arcs.

Clearly, if these characters are as important as I believe (particularly the last), then the affinities of *P. granifera* and *formosa* are with *Nepanthia* (and especially with species such as *N. crassa* and *N. belcheri* with thicker body-walls and more numerous secondary abactinal plates) rather than with *Patiria* sensu Gray, 1840—now synonymized with *Asterina*. However, this contradicts Fisher's conclusion of 1941 that *granifera* is close to *Patiria miniata* but *crassa* is allied with *Nepanthia*. If Fisher's evaluation of the affinities is correct and at least a generic distinction should be recognized between *granifera* and *crassa*, then *Callopatiria* needs to be revived for *P. granifera* and *formosa*. The zoogeographical separation, with the westernmost record for *Nepanthia* being from Burma, supports such a distinction but the morphological characters are individually relatively unimportant. They include the following: In the two South African species the arms are less well defined basally so that the interradiar arcs are rounded or only bluntly angled; the superomarginal plates appear to match the inferomarginals in size during growth, the successive ones remaining contiguous whereas in most *Nepanthias* seen the superomarginals are smaller, some of them being separated by interstitial abactinal plates and in *N. briareus*, which has particularly cylindrical arms and ill-defined ventrolateral angles, the superomarginals outnumber and fail to match the inferomarginals; the actinal armament is much more coarse while the spinelets





**Fig. 7** *Allopatiria ocellifera* (Gray), BM reg. no. 1969.12.16.13, Cape Lever, Mauritania, R 38 mm (the uppermost ray denuded),  $\times 1\frac{1}{2}$  (above); '*Patiria*' *obtusa* Gray, holotype, 1938.6.23.24, Panama, R up to 54 mm (the lower right ray partly denuded, and a few plates lost)  $\times 1\frac{1}{2}$  (middle), side view of detached arm, partly denuded, of the same,  $\times 3$  (below).



of at least the proximal plates usually number less than ten and form single or double fans, especially in *formosa*, rather than being very fine and forming dense clusters as in the species of *Nepanthia*; lastly, the development of the superambulacral plates is less advanced, as outlined above. Cumulatively, these differences probably do justify the revival of *Callopatiria* with generic rank but the relationship with *Nepanthia* merits further attention. That genus has already been broadened in concept considerably by the inclusion of *Parasterina crassa* with its very thick body wall and complex abactinal skeletal structure.

The only remaining species of *Patiria* is *P. obtusa* Gray, 1847. The poorly preserved holotype (Fig. 7 below) with its relatively long arms (R/r 53/17 mm = 3.1/1) and irregular abactinal plating (possibly at least partly due to the condition) appears very unlike an *Asterina* but superficially resembles *Callopatiria granifera*, with which Verrill (1913) considered it congeneric. However, the similarity does not extend to the internal characters since the broken arm shows a complete absence of any superambulacra or other internal reinforcing plates. The inferomarginals are relatively large, appearing pearshaped in the section view (Fig. 5a) but flattened and tapering externally to appear long oval on the surface; their relatively ventral position is probably due to the unnatural flattening of the specimen and this may also account for the rounded ventro-lateral profile. The species is not a ganeriid since the marginals are not at all blocklike, the adjacent abactinal and actinal plates are strongly imbricating so as to reinforce the ventrolateral area, quite unlike those individuals of *Cyathra* with marginals reduced to this same small superficial size. Without more material in better condition, a proper assessment of the position of '*Patiria*' *obtusa* among the asterinids cannot be made. The species is known only from the holotype, Verrill's near-pentagonal specimen from Panama recorded under this name (1869) with its relatively sparse actinal armament (rather than dense clusters of spinelets) being some other asterinid (perhaps *Enoplopatiria siderea* Verrill, 1913, also from Panama). Neither H. L. Clark (1940) in the echinoderms of the *Zaca* expedition to west Central America, nor A. H. Clark (1946) in the echinoderms of the Pearl Islands, Bay of Panama, recorded *obtusa*, so there must be an element of doubt about its source.

The name *Asterinopsis* has been declared invalid by H. L. Clark (1938), since Mortensen (1933) noted that Lamarck's material of the type species is lost and its precise locality was uncertain. H. L. Clark noted that the two Atlantic species included in *Asterinopsis* by Verrill: *Asterina lymani* and *A. pilosa* of Perrier, 1881, are not congeneric with the Indo-Pacific species subsequently included, leaving them in limbo when he transferred some of the non-Atlantic species to *Paranepanthia* Fisher, 1917.

Finally, *Allopatiria* was for long of uncertain value, owing to ignorance of the type locality of the only species, *Patiria ocellifera* Gray, Verrill's supposition of Australia being unsubstantiated. In 1963 I redescribed the holotype, prompted by Professor Tortonese who had just discovered a similar specimen from the Mediterranean and who subsequently (1963) synonymized with *A. ocellifera* the Mauritanian *Parasterina africana* Engel & Croes, 1960. I believe that both *Patiria rosea* and *P. pulla* Koehler & Vaney, 1906, again from Mauritania, are also synonyms of *A. ocellifera*. Apart from colour differences in the type specimens (pink/red as opposed to grey with yellow spots) these two were supposed to differ from one another by minor differences in the body shape, the denuded condition of some of the enlarged abactinal plates in the holotype of *rosea* and different degrees of prominence of the furrow spines—the last two almost certainly due to artefacts of preservation. Madsen (1950) has already suggested that these differences are only individual variations when he provisionally synonymized *pulla* with *rosea*. The figures of *rosea* (1906, pl. 5, figs 3, 4) show a considerable resemblance to the holotype of *A. ocellifera* illustrated in A.M.C. (1963, pls 1, 4), despite the much larger size of the latter (R c.80 mm as opposed to 43 mm in the holotype of *rosea*).

*Allopatiria ocellifera* has a very distinctive abactinal skeleton with extremely numerous secondary plates (at least at R > 30 mm), many of them superimposed on the primary plates (or at least their peripheral parts), so that only rounded areas of most of the radial 'field' primaries of the rays are not overlain (Fig. 3g). The armament of the primaries (when intact)

is a dense covering of short blunt spinelets, though the secondaries often bear a high proportion of two- or three-valved spiniform pedicellariae. *Asterina stellifera* also has similar pedicellariae, body form and large maximum size (R max. > 50 mm) and occurs in West Africa to the south of Cape Verde, as well as on the east coast of South America. Despite these factors, I think that Verrill's generic distinction is well justified. *A. stellifera* and the other species of *Asterina* have short but broad midradial primary abactinals, many of them with a more or less well marked double concavity in the proximal side formed by three lobes of varying prominence and the other primaries of the pore areas are clearly crescentiform. A relatively small specimen of *Allopatiria ocellifera* (a paratype of *Parasterina africana*) with R 17 mm has three longitudinal series of apparently round primary plates on the radial 'fields', the more proximal ones revealed as rhombic when the spinelets are removed, the widest part being at the middle of the length. These plates just imbricate at the angles and the secondaries are limited to the interstitial rounded popular areas between them, numbering up to five in each area. The distal primaries, especially of the two outer series, become relatively broad and short and their armament resolves itself into two transverse linear series of spinelets. As growth proceeds, the secondaries become much more numerous, encircling the primaries and then encroaching progressively on their upper surface so that at R 80 mm (possibly before) only some of the distalmost primaries (which have become relatively large and rounded) are exposed except for their spinelets (A.M.C., 1963). This highly modified abactinal skeleton I believe fully justifies retention of a generic distinction for *Allopatiria* as suggested by Tortonese (1963).

Before revised diagnoses can be given of the families Ganeriidae and Asterinidae in the light of the present comments, it is necessary to describe a new aberrant genus of Asterinidae.

### Genus *PAXILLASTERINA* nov.

**DIAGNOSIS.** A genus of Asterinidae with very flat, almost pentagonal, body form; primary abactinal plates not arranged in distinct radial and lateral 'fields' but regularly arranged, thin and flat except for an abrupt, short, flat-topped central column on many plates, including the midradial row of proximally 3-lobed plates, the columns replaced on others—especially the first adradial row each side of the midradial row—by a smaller rounded convexity, all these elevations crowned by a tall pompom or rounded tuft of numerous slender spinelets which are embedded in a soft matrix so as to radiate from a central conical core and not articulate directly with the elevation on the plate; only a few small secondary abactinal plates present proximally; margin very thin, formed by the inferomarginal plates only, the superomarginals small and inset dorsally; actinal and adambulacral plates armed with relatively few (<6) slender spinelets webbed together into fans; no pedicellariae observed.

**TYPE SPECIES.** *Paxillasterina pompom* sp. nov.

**REMARKS.** Superficially the small asterinid on which this new genus is based (R only c. 15 mm in the four specimens) resembles the flatter, more nearly pentagonal species of *Asterina* such as *A. folium* (Lütken) but is marked off on closer scrutiny by the many paxilliform abactinal plates and their peculiar armament. It should be noted that in poorly-preserved and especially in dried specimens the pompoms contract and may become appressed on to the surface and the low paxillar columns can only be appreciated when the skeleton is denuded. Possibly similar specimens have been collected and attributed to the common Caribbean *A. folium*, this modification having been overlooked. It necessitates an alteration to the diagnosis of the Asterinidae in which truly paxilliform plates were not previously known. Conversely the diagnosis of the Ganeriidae also needs to be qualified to allow for the non-paxilliform plates of individuals of *Cycethra verrucosa* such as were previously referred to *Patiria obesa*.



*Paxillasterina pompom* sp. nov.

Figs 8, 9

HOLOTYPE. Korbiski Reef, San Blas Is, off Atlantic Panama east of the Canal Zone, c.6 m., under coral rubble. Collected by Dr G. Hendler.

R/r 14/11 mm = 1.3/1. The form is pentagonal, the body thin with central height only 5 mm (including the armament). The primary abactinal plates are very regularly arranged in rows parallel to the radii (or in chevrons if regarded interradially), and there is no distinction of radial and lateral 'fields' of plates, though the more adradial plates have the superficial part crescentic visible when denuded, subtending a single papular pore, except for the plates of the mid-radial row which have a median proximal lobe and a double concavity subtending two pores, the more lateral plates rhombic or fan-shaped; all these plates rather thin with only an inconspicuous texturing of crystal bodies and flat except for a central elevation which takes the form of a well-defined but low flat-topped column on many plates, including all of the midradial row and most of the second adradial each side, as well as scattered other plates; these columns crowned by a tall ovate pompom of numerous fine needle-like spinelets numbering up to c.50 and embedded in a soft matrix so that their bases arise from a central uncalcified cone and not directly from the column; other primary plates, including the first adradial row, have a small rounded central convexity bearing a smaller pompom in proportion, some plates adjoining the superomarginals having as few as 6 spinelets in the cluster; one or two small secondary abactinal plates occur around some of the proximal papular pores; there are 10 longitudinal rows of pores on each ray, the outermost of only 4 pores. The superomarginal plates are mostly smaller than the adjoining abactinal plates and are rounded or D-shaped; each bears a small pompom, the more interradiial ones with up to c.15 spinelets. The inferomarginal plates project well beyond the superomarginals to form the edge of the body, their adradial parts are flattened dorso-ventrally but the free part is prolonged and constricted so as to be rounded in cross section and separated from the adjacent inferomarginals; each bears a laterally compressed cluster of numerous fine spinelets, the apical ones slightly coarser than the abactinal spinelets. The actinal plates are in regular

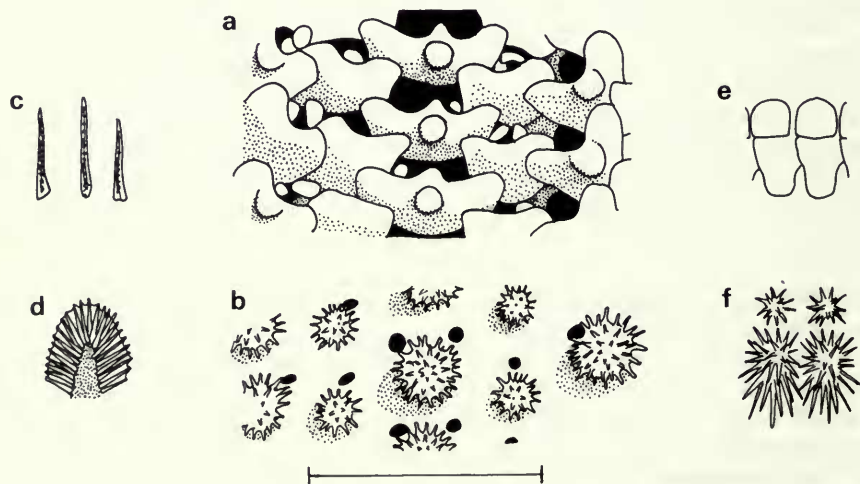


Fig. 8 *Paxillasterina pompom* gen. & sp. nov., holotype, USNM, Korbiski Reef, Atlantic side of Panama, R 14 mm (a) and (b) parts of denuded and intact proximal abactinal midradial areas; (c) three paxillar spinelets; (d) vertical section of one pompom (detached from column); (e) and (f) two pairs of marginal plates in dorsal view, denuded and intact (proximal to the left). The scale measures 1 mm for (c) and 2 mm for the rest.



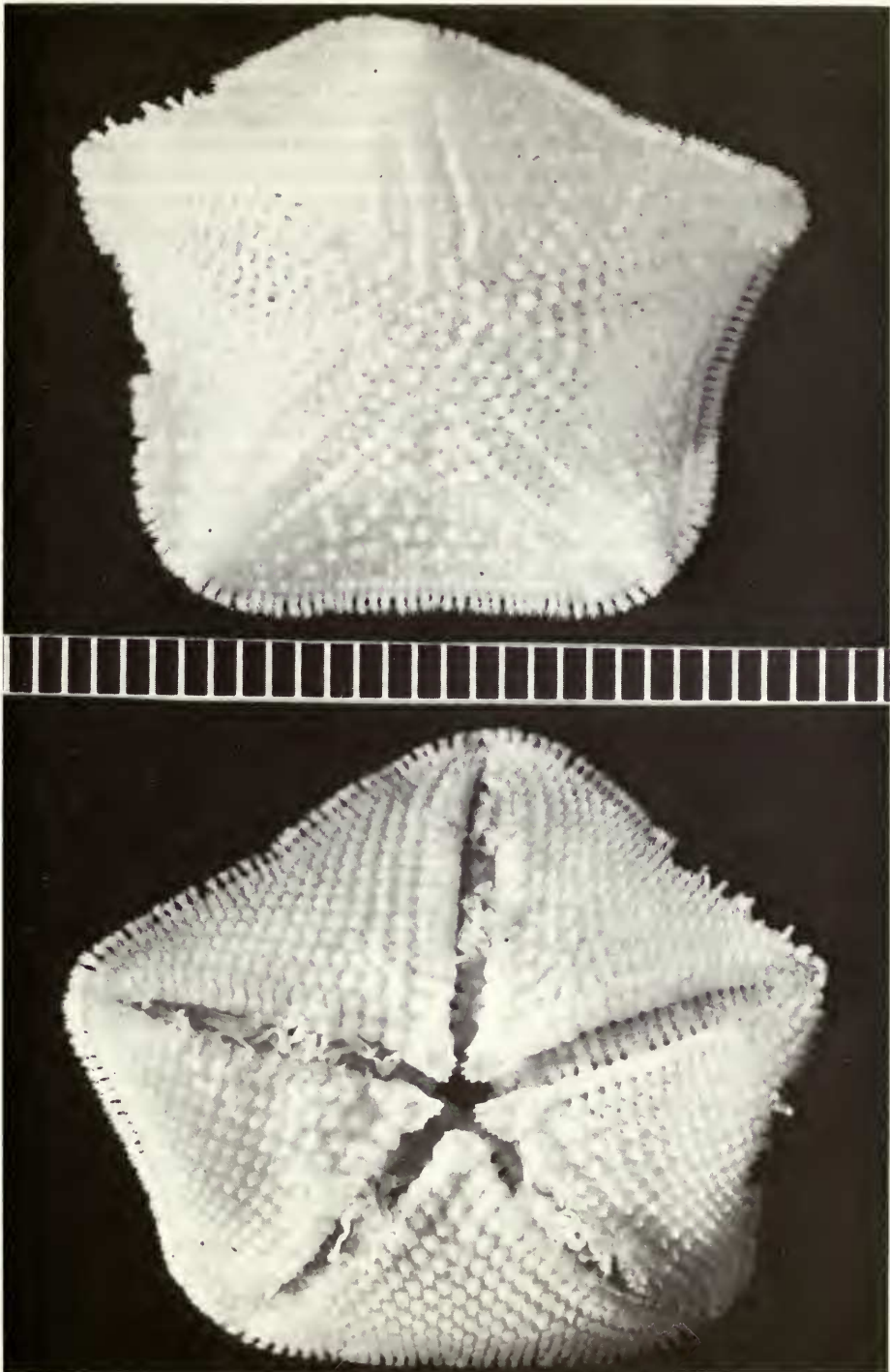


Fig. 9 *Paxillasterina pompom*, holotype, from above and below,  $\times 4$ .

chevrons and each has two or three adradial lobes (distinct when denuded); each bears a tangentially-aligned fan of up to 5 spinelets, mostly 3 but the admarginal ones with 5, joined by skin. The adambulacral plates each have a shallow abradial step bearing a fan of subambulacral spinelets aligned slightly obliquely to the furrow and close behind the fan of furrow spines, which are slightly longer but arise at a higher level so that the tips project to about the same extent; each fan is usually of 4 spines or spinelets and webbed. Each jaw is armed with a larger fan of up to 16 spines, 7 or 8 on each oral plate, the apical ones about twice as large as the outermost; there is also a pair (or trio) of small suboral spinelets on each plate. The gonopores cannot be distinguished.

**PARATYPES:** Three other specimens are also available from the Atlantic side of Panama. One is also from Korbiski Reef but in 3 metres depth; it has R/r 15/11.5 mm and is similar to the holotype but for having usually 5 furrow spines. Another, from Mackerel Reef, also San Blas Is, was only collected two years ago and still shows traces of yellow colouration in spirit. The third is from 'Landing Craft Reef', south of the Galeta Marine Laboratory, Canal Zone, 'under rock in the coralline zone or higher'; it is dried and distorted with the pompoms mostly appressed horizontally; R is c.10 mm and the subambulacral spinelets usually number only 3.

### Family GANERIIDAE Sladen

Asterinidae: Ganeriinae Sladen, 1889: 375–376.

Ganeriidae: Perrier, 1894: 171; Fisher, 1911a: 251 (in key); Verrill, 1914b: 365–366; Fisher, 1940: 127; A. M. Clark, 1962: 23–24; Bernasconi, 1964: 59–60; Spencer & Wright, 1966: U69; Blake, 1981: 380–381 (pt). [Non Ganeriidae: A. H. Clark, 1938, Downey, 1973 (*Leilaster*)]

Asterinidae (pt): Madsen, 1956: 22–23; Bernasconi, 1973: 335–336 (*Patiria obesa*).

Goniasteridae (pt): Bernasconi, 1965: 333–335 (*Vemaster*).

A family of Valvatida with body stellate, rarely almost pentagonal, interradian arcs rounded, arms normally five, rounded in cross-section except in the aberrant abyssal *Vemaster*; abactinal plates imbricating, usually paxilliform but the columns sometimes broadened and not well-defined, or coarse and tabulate, or with the basal lobes reduced and the plates obscured by thickened pustular body wall (in wet specimens of *Perknaster*), crowned with clusters of spinelets, which may be short and superficially appearing granuliform in *Ganeria*, some specimens of *Cycethra* and in *Vemaster*; papulae in small groups in the meshes between the primary plates, more numerous adradially; marginal plates ranging from blocklike and conspicuous to indistinguishable from the adjacent plates, aligned laterally or towards the ventral side when smaller (as usually in *Perknaster*), reduced to one slightly projecting series (presumed inferomarginals) in *Vemaster*, armed with oval groups of spinelets or spines, or one or two vertical combs when coarser, as in *Ganeria*; actinal plates imbricating adradially, tending to form oblique transverse as well as longitudinal rows, especially the latter, each armed with a group of spinelets or one or two larger spines, except in *Vemaster* where armament is rare and the plates are irregular and possibly secondary and limited to the interradian; adambulacral plates small, matching the adradial row of actinal plates, armed with two (or sometimes one) furrow spines and several subambulacral spines, often forming pairs parallel (or oblique) to the furrow or all the spines forming one (or two) series transverse to the furrow; pedicellariae absent (rarely a few spinelets forming a simple fascicle); internally a proximal interradian calcified pillar supporting the abactinal body wall dorsolaterally, no superambulacral plates.

### Family ASTERINIDAE Gray

Asterinidae Gray, 1840: 228; Perrier, 1875: 27–28[292]; Sladen, 1889: 374–376; Fisher, 1911a: 253–254; Verrill, 1913: 477–481; 1914b: 262–263; 364–365; Fisher, 1919: 409; Madsen, 1956: 22–23; Spencer & Wright, 1966: U68; Bernasconi, 1973: 335–336; A. M. Clark & Courtman-Stock, 1976: 75; Blake, 1981: 380–391 (pt).

A family of Valvatida with body form usually pentagonal to stellate but sometimes the rays narrow and more or less finger-like, usually numbering five but occasionally more, the surface completely flat below (unless the whole body is arched upwards when it is concave) but variously convex above, ranging from very low, the body leaf-like, to high with almost cylindrical rays but still with a distinct ventro-lateral angle supported internally by overlapping extensions of the lateralmost abactinal and actinal plates, the angle culminating in the relatively small inferomarginals, or sometimes blunted by similar prominence of both marginal series (in *Nepanthia* and *Callopatiria*); abactinal plates superficially flattened or convex, sometimes with a low ridge bearing the armament and in one case (*Paxillasterina* nov.) with a low circular paxillar column, the primary radial and interrarial plates of the disc often distinguishable by their regular shape, the larger lobed more adradial plates of the papular areas appearing more or less crescentic, imbricating adradially (the more lateral plates) or proximally (the more midradial plates), often two magnitudes of plates, at least adradially, with much smaller secondary plates subdividing or restricting the papular spaces proximal to the primary plates, often with considerable regularity of arrangement of all the plates, though this tends to become obscured in large specimens; abactinal armament of multiple small spinelets, sometimes granules, on the middle or raised part of the plate, or armament lacking when the skin is more or less thickened; papulae usually single, sometimes in small clusters, absent near the margin; superomarginal plates small, often distinguishable from the adjacent abactinal plates only by their position above (sometimes alternating with) the inferomarginal plates which are seen in transverse sections of the ray to be wedge- or pear-shaped or peg-like, appearing as a reversed keystone wedged in among the overlapping inner ends of the adjacent lateralmost abactinal and actinal plates, but in external view appear oval or rectangular; the very flattened genera *Anseropoda* (and probably also *Stegnaster* and *Tremaster*) with less massive reinforcement for the very narrow angle, the entire body except for a narrow midradial band strengthened by overlapping struts projecting from the abactinal and corresponding actinal plates to form a latticework; actinal plates imbricating adradially, forming more or less regular transverse or oblique series from furrow to margin, also tending to form longitudinal rows parallel to the furrow but the abradial plates sometimes irregular, armed with one or several spinelets, when multiple arranged in fans or clusters: adambulacral plates relatively small, matching the innermost actinal rows and with armament usually of similar magnitude, furrow spines in a fan or comb; pedicellariae, if present, usually simple alveolar with two, occasionally three, slightly curved spiniform valves, sometimes (*Nepanthia*) fasciculate with more numerous valves; internally a proximal interrarial pillar supporting the abactinal body wall; superambulacral-like plates developed more or less regularly in the narrow-rayed genera *Nepanthia* and *Callopatiria* but absent elsewhere.

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### Synopsis

*Leilaster* A. H. Clark, 1938 (family Ganeriidae) and *Mirastrella* Fisher, 1940 (family Asterinidae) are abstracted from these families and provisionally referred to the order Spinulosida, family yet to be determined.

*Vemaster* Bernasconi, 1965, is referred from the Goniasteridae to the Ganeriidae but may warrant isolation in a suprageneric taxon when the whole family is reviewed.

*Patiria obesa* (H. L. Clark, 1910) is found not to be an asterinid but is synonymized with *Cycethra verrucosa* (Philippi, 1857), family Ganeriidae.



*Patiria* Gray, 1840, type species: *P. miniata* (Brandt, 1835) is synonymized with *Asterina* Nardo, 1834.

*Patiria miniata* (Brandt, 1835), *P. pectinifera* (Müller & Troschel, 1842), *P. chilensis* (Lütken, 1859) and *P. stellifera* (Möbius, 1859), are referred to *Asterina*.

*Patiria granulosa* (Perrier, 1875) is a synonym of *Asterina miniata* (Brandt, 1835).

*Patiria granifera* Gray, 1847 and *P. formosa* (Mortensen, 1933) are referred to *Callopatiria* Verrill, 1913, revived.

*Patiria pulla* and *P. rosea* Koehler & Vaney, 1906, are synonymized with *Allopatiria ocellifera* (Gray, 1847).

*Paxillasterina* gen. nov. for type sp. *P. pompom* sp. nov. from Atlantic Panama is described.

The following taxa are thought to be in need of reassessment:

Ganeriidae: *Aleutiaster* A. H. Clark, 1939

*Hyalinothrix* Fisher, 1911b

*Knightaster* H. E. S. Clark, 1972

*Tarachaster* Fisher, 1913.

Asterinidae: *Patiriella* Verrill, 1867

'*Patiria*' *obtusa* Gray, 1847

'*Enoplopatiria*' *siderea* Verrill, 1913

### Appendix—The generic name *Asterina* and its type-species

The first use of the name *Asterina* was by Nardo (1834 : 716) for the two species *Asterias minuta* Linnaeus and *A. exigua* Lamarck, neither one designated as type species. In 1836 L. Agassiz adopted *Asterina* Nardo and cited only *Asterias minuta* Linnaeus. The first formal type designation now traced is the apparently provisional one of Fisher (1906 : 1087) stating 'Type (?) *Asterina gibbosa* (Pennant). *Asterina minuta* (Olivi) Nardo = *Asterias gibbosa*', repeated without the query and abbreviated to '*Asterias minuta* Olivi = *Asterias gibbosa* Pennant' by Fisher in 1911a : 254, while Verrill (1913 : 479) modified it to '*A. minuta* Nardo = *A. gibbosa* (Pennant)'. *Asterias minuta* Linnaeus dates from the Fauna Svecica (1761 : 512) and was described from Norwegian waters in terms mainly comparative with *Asterias rubens*. In the 12th and 13th (Gmelin) editions of the 'Systema naturae' (1767 and 1791) the concept of *A. minuta* was extended to include first the *Asterina*-like seastar from American waters shown in pl. 5, figs 14 and 15 of Seba (1758) and then *A. minuta*: O. F. Müller, 1776, again from Scandinavia, and *A. minuta*: Fabricius, 1780, from Greenland. In none of these localities does the common European starlet widely known as *Asterina gibbosa* occur and Verrill (1914a) notes of [*A*] *minuta* Linnaeus, 1761 'There is nothing in the few words of description to show that it is not the young of *A. rubens* or some similar species.' At first sight, this appears to render *Asterina* Nardo a synonym of *Asterias* Linnaeus.

However, it is evident that Fisher was aware of this anomaly, hence his introduction of '*Asterias minuta* Olivi' (1792), a record from the Adriatic where *gibbosa* is found (also the recently recognized *Asterina phylactica* Emson & Crump but that diminutive species may be ignored in this context). Articles 69 and 70 of the Code of Nomenclature, on subsequent designation of type-species and deliberate use of misidentification, are intended to allow for this sort of problem so that the species which Fisher had in mind—namely *Asterias gibbosa* Pennant, 1777—is usable as type-species of *Asterina* Nardo. Evidence that this concept of *Asterina* is in accord with Nardo's lies in Forbes' use of *Asterina gibbosa* already in 1839.

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